AMERICAN MUSEUM NOVITATES

Number 1004 Published by THE AMERICAN MUSEUM OF NATURAL HISTORY New York City December 28, 1938

NORTH AMERICAN RHABDOCOELA AND ALLOEOCOELA. II[1]

REDISCOVERY OF *HYDROLIMAX GRISEA* HALDEMAN

BY LIBBIE H. HYMAN

In the spring of 1935, Professor Dahlgren of Princeton University requested me to attempt the identification of an unusual and interesting turbellarian which he had noticed appearing in abundance every spring in fresh-water habitats in the vicinity of Princeton. After examining the beautifully prepared serial sections sent me by Professor Dahlgren I reported that the animal was an alloeocoel of the family Plagiostomidae and that I believed it to be new and to merit the creation of a new genus. Later through the kindness of Professor Dahlgren I saw the animal alive in its natural habitat. We found many large red-brown capsules similar to those of planarians plastered to the under surface of the stones frequented by the animal. These were shown to be the capsules of the plagiostomid as they hatched in a couple of weeks into small worms resembling the parent forms in all respects. The life-cycle of the animal then appears to be as follows. The sexually mature plagiostomids come to the shallower parts of their habitats in the spring to lay their egg capsules and then die. The young hatching from these capsules return to the normal habitat, the muddy bottoms of old slow streams. By the following spring they have grown to sexual maturity and again seek the shores for breeding purposes.

While looking through some old papers on American Turbellaria, I accidentally discovered that this plagiostomid had been seen before and that in fact it was at one time very abundant in old streams in eastern Pennsylvania and New Jersey. The species was discovered by Haldeman in 1842 and named by him *Hydrolimax grisea*. Haldeman apparently thought the animal was some sort of slug. He described correctly the color pattern and the positions of the mouth and the genital pore, mistaking the latter for a mucous pore. Later and independently, Leidy (1851), from whose sharp eyes no fresh-water invertebrate seems to have escaped, found the animal in abundance in the Delaware and

[1] The first paper of this series of articles was published in 1936, in Trans. Amer. Micro. Soc., LV, pp. 14–20, under the title: 'Studies on the Rhabdocoela of North America.'

Schuylkill rivers and being unaware of Haldeman's description, renamed it *Cathesia stellato-maculata*. The specific name refers to the stellate pigment spots. Girard, in his résumé of North American planarians (1893), called attention to the identity of Leidy's and Haldeman's species and gave some recognizable figures of *Hydrolimax grisea*. I have been unable to find any mention of the animal since Girard's publication and apparently the species has disappeared from most of its former habitats because of pollution of the water.

The family Plagiostomidae is a well-known family of small alloeocoelous Turbellaria, chiefly marine, comprising a considerable number of species, most of which fall into the genus *Plagiostomum*. Of the few known fresh-water plagiostomids, *Plagiostomum lemani*, from central European lakes, especially the Swiss lakes, is the commonest and has received the most attention. *Hydrolimax grisea* is the first fresh-water plagiostomid to be found in North America; some other fresh-water alloeocoels are, however, known for this continent, such as prorhynchids and *Bothrioplana*. The more important references on the anatomy and systematics of the Plagiostomidae are: Böhmig (1890), Hofsten (1907), Graff (1911, 1913), Bock (1923), and Brandtner (1934). *Hydrolimax* adds another genus to the previously recognized genera of the family: *Plagiostomum* O. Schmidt, 1852; *Alvaera* Bock, 1923 (= Hallezia Graff, 1908); and *Brachyposthia* Brandtner, 1934.

Hydrolimax grisea Haldeman

Hydrolimax grisea HALDEMAN, 1842, Proc. Acad. Nat. Sci. Phila., I, p. 166.
Cathesia stellato-maculata LEIDY, 1851, Acad. Nat. Sci. Phila., V, p. 289.
Hydrolimax griseus HALDEMAN, GIRARD, 1893, Ann. Sci. Natur., (7) XV, p. 161.

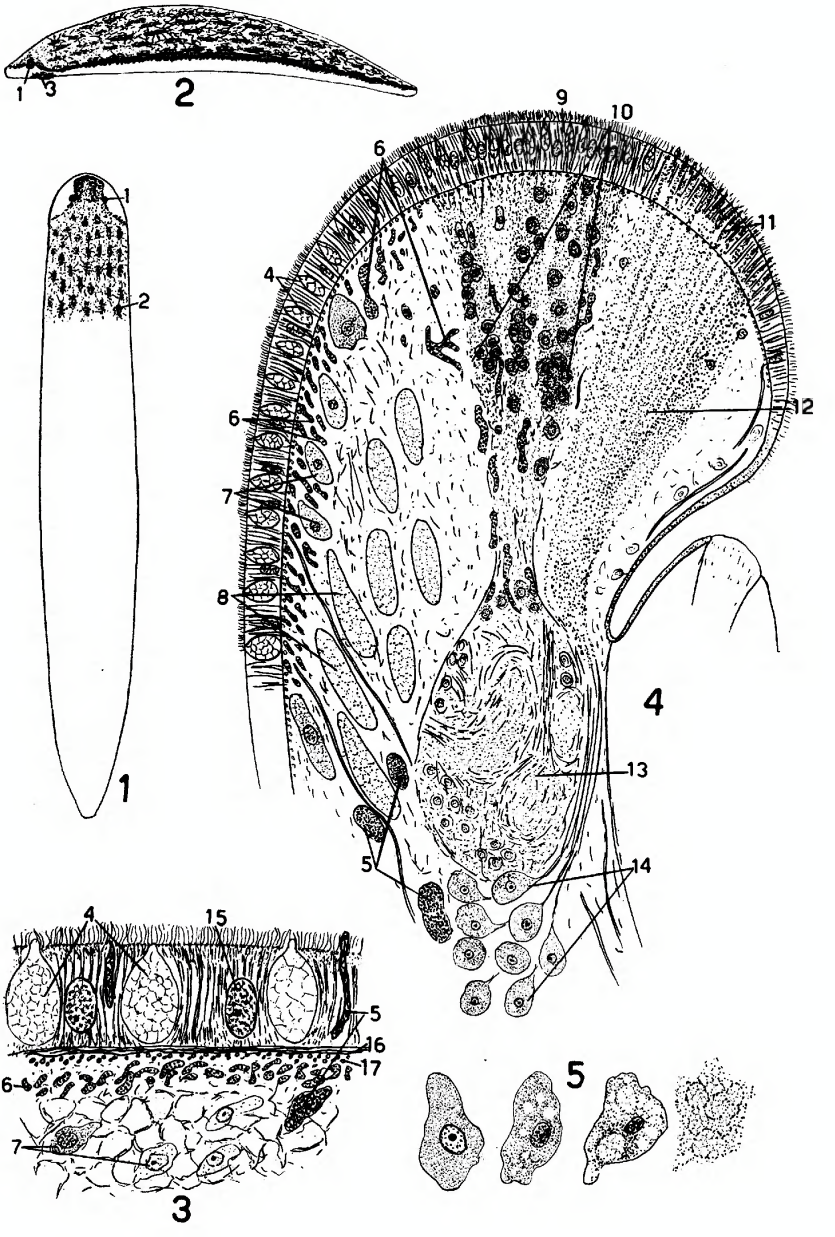
The following account is confined to the anatomy and histology of *Hydrolimax* as Professor Dahlgren will write a separate account of the general habits, breeding and egg-laying, ovogenesis and early development, matters which have proved exceptionally interesting. The abundance of this species in the spring at Princeton has furnished an unusual opportunity to make a thorough study of a representative of a group ordinarily found only in small numbers.

1. EXTERNAL CHARACTERS.—*H. grisea* is an unusually large alloeocoel, attaining a length of 13–15 mm., although the majority of mature specimens are somewhat smaller than this. The body is soft, slimy, and plump, flattened below, highly rounded above, tapering to a rounded anterior end, and a more pointed posterior end (Figs. 1 and 2). The color is dark gray above, seen to consist on magnification of oval

dark pigment-spots connected with each other by spidery pigment-lines. At the anterior end the color narrows suddenly and extends to the anterior end only between the eyes. The lower surface is white and the white color at the anterior end continues onto the dorsal surface as a crescentic white area to either side of the median dark band. The boundary between white and gray is very sharp and gives the anterior end an unmistakable appearance with its gray center and white sides (Figs. 1 and 2). At the boundary of the gray and white areas on the head are seen the eyes, a pair of black ovals so deeply set as to be inconspicuous. They were missed by Haldeman but seen by Leidy and Girard. The general appearance is that of a miniature gray slug but the type of locomotion is not sluglike. The animal progresses rapidly in the smooth gliding manner characteristic of the smaller Turbellaria, caused by ciliary action. Owing to its plump, cylindroid shape, it rolls from side to side as it moves and is easily turned over.

The conspicuous mouth is located on the ventral side of the head (Fig. 2) and the common genital pore is found near the posterior extremity on the ventral surface (Fig. 14).

2. Epidermis.—The body is clothed in a columnar epithelium, here called epidermis. It is ciliated throughout and appears to be syncytial, as noted for various alloeocoels by other observers; at least it is impossible to find any definite cell walls in the best available sections. The free border consists of the basal bodies of the cilia (Fig. 3). The epithelium itself seems to be composed of parallel strands extending from the free border to the basement membrane (Figs. 3, 4). A similar structure has been described for the epidermis of other plagiostomids by Böhmig, Hofsten, Brandtner, etc. Between these strands are elongated clear spaces called vacuoles by German workers. They have no definite walls in *Hydrolimax* and appear to be simply transparent ground substance in which the strands are imbedded. At intervals throughout the epidermis are seen the large nuclei whose size precludes the possibility that the strands could represent the walls of very narrow cells. The epidermis contains numerous large oval bodies which discharge through the surface (Figs. 3, 4). These bodies, termed "wasserklaren Räumen" by Böhmig, are in my sections of *Hydrolimax* obviously containers of a mucous secretion which forms a network in the interior. These slime reservoirs, as I shall call them, do not seem to be cells. German workers have failed to find any parenchymal gland cells with which they are connected, but I believe that in *Hydrolimax* they are related to certain large cells seen in the parenchyma adjacent to the epidermis (Figs. 3, 4).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My reason for so thinking is that near the dorsal epidermis of the anterior end, where the slime reservoirs are particularly abundant, there occur in the adjacent parenchyma very large bodies having the same appearance as the reservoirs (Fig. 4). Transitional stages can be found between these bodies and the large cells just mentioned. It thus seems probable to me that the large cells alter and enlarge into slime bodies (Fig. 5) and these discharge by means of the slime reservoirs. In addition to the slime reservoirs the epidermis is perforated by the outlets of cyanophilous gland cells located in the parenchyma. These are coarsely granular cells which stain a deep blue in Mallory's triple stain. Rhabdites appear to be absent in *Hydrolimax*.

The epidermis is slightly taller at the two body extremities than elsewhere. At the anterior tip just above the mouth this taller epidermis is punctured by the numerous outlets of the frontal glands (see below) as shown in figure 4. Just dorsal to this region is a zone of sensory epidermis connected with the brain by a conspicuous ganglionated tract containing many ganglion cells (Fig. 4). This sensory epidermis does not differ as far as could be determined on the available sections from the epidermis elsewhere but it must be assumed that it contains sensory endings of some sort. The sensory epidermis, like the general epidermis, is filled with slime reservoirs which are here much smaller than elsewhere. Posterior to the sensory region, the epidermis contains a great abundance of slime reservoirs which stain more deeply than elsewhere and so are particularly conspicuous. It is in this region above the brain that one can find most easily transitional stages between the large parenchymal cells mentioned above and slime bodies (Fig. 5). First vacuoles

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Fig. 1. Dorsal view of *Hydrolimax grisea* from life. Pigmentation is shown for only a small area.

Fig. 2 Side view of *Hydrolimax grisea* from life.

Fig. 3. Small portion of a section to show structure of epidermis and adjacent parts.

Fig. 4. Sagittal section of the anterior end.

Fig. 5. Different appearances of large sub-epidermal cells believed to represent stages in the transformation of such cells into mucous-containing networks.

1, eye; *2*, pigment spots; *3*, mouth; *4*, slime reservoir; *5*, cyanophilous gland; *6*, pigment bodies; *7*, large sub-epidermal cells; *8*, mucous stages of the same; *9*, sensory area at tip of head; *10*, ganglionated tract to same; *11*, exits of frontal glands; *12*, bundle of ducts of frontal glands; *13*, brain; *14*, cluster of frontal gland cells; *15*, nucleus of epidermis; *16*, circular sub-epidermal muscle layer; *17*, longitudinal sub-epidermal muscle layer.

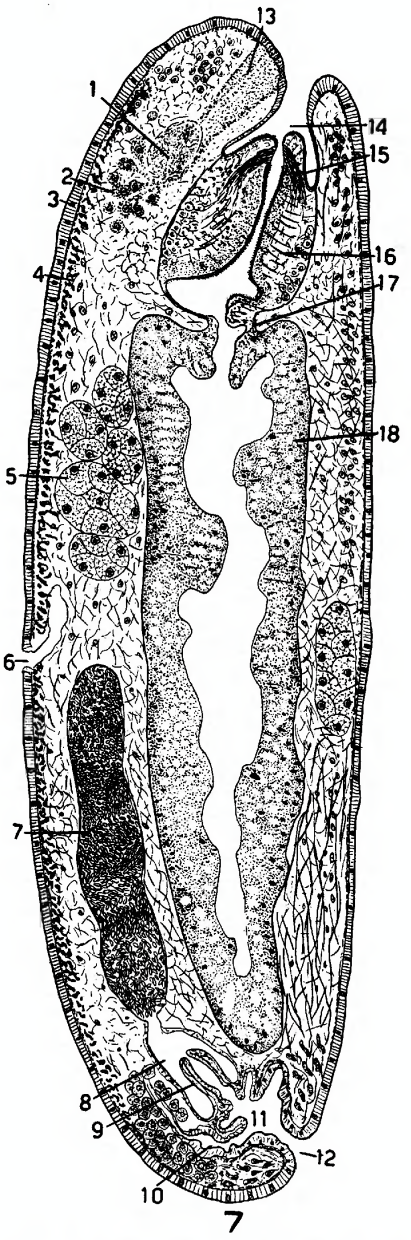
appear in the large cells, their nuclei become condensed and shrunken, and eventually the entire cell is converted into a vacuolated mass with ill-defined contours, without a nucleus, and staining like mucous (Mallory's triple stain). Several cells seem to fuse together to form one of these large mucous masses. Indications of a connection of the mucous masses with the slime reservoirs have been seen. Stages shown in figure 5 can be found everywhere beneath the epidermis, but they are less numerous than in the parenchyma dorsal to the brain. The evidence indicates that the slime reservoirs are the outlets of parenchymal slime bodies which in turn represent transformed parenchymal cells.

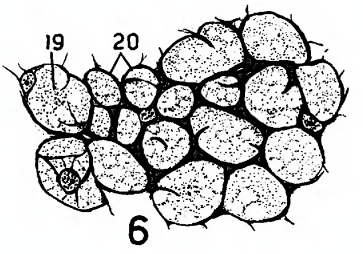
The epidermis of *Hydrolimax* is evidently adapted for secreting large amounts of slime on short notice through its slime reservoirs. These apparently substitute for rhabdites.

At the posterior end around the genital pore the epidermis is perforated by the exits of the numerous caudal glands, eosinophilous glands located in the adjacent parenchyma. They take a brilliant pink stain in eosin or acid fuchsin and are probably concerned in egg-laying, presumably secreting the cement by which the capsules are attached to objects. They also are generally supposed to function as a holdfast during locomotion.

3. Sub-epidermal Structures and Parenchyma.—Beneath the basement membrane of the epidermis is found the usual sub-epidermal muscle sheath characteristic of the Turbellaria. In *Hydrolimax* it consists of two very thin strata, an outer circular and an inner longitudinal layer (Fig. 3). Internal to the muscle sheath are seen on the dorsal side the pigment bodies, small masses of various shapes filled with black spherules. Whether these are cells could not be determined. Pigment bodies also occur in the interior along the large sensory tract extending from the anterior epidermis to the brain (Fig. 4).

All interior space not occupied by the digestive tract and the reproductive system is filled with parenchyma. The parenchyma of *Hydrolimax* conforms to Böhmig's account of that of other plagiostomids, consisting of alveoli of a firm homogeneous substance inclosing a more fluid, faintly granular material (Fig. 6). Nuclei are present here and there in the angles of the network. Besides the structures already described, such as the pigment bodies and the cells and masses related to the slime reservoirs, the parenchyma contains a few muscle fibers, mostly longitudinal, and several sorts of gland cells. The gland cells of the Turbellaria, according to the analysis of German specialists, consist of two main types, eosinophilous and cyanophilous. The former stain with eosin or





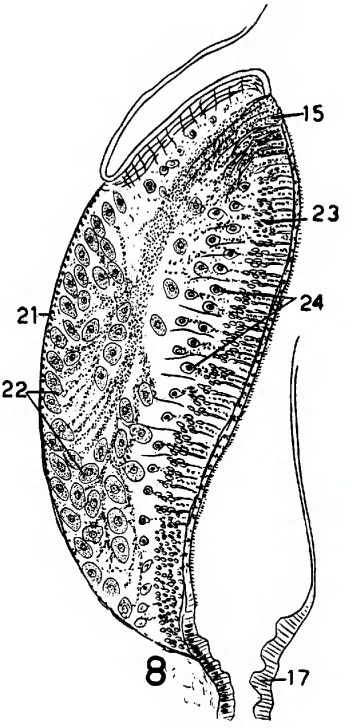


Fig. 6. Parenchyma of *Hydrolimax grisea.*

Fig. 7. Sagittal section of *Hydrolimax grisea.*

Fig. 8 Sagittal section of the pharynx, only dorsal half shown.

1, brain; *2*, frontal glands; *3*, epidermis; *4*, pigment layer; *5*, yolk glands; *6*, mid-dorsal excretory pore; *7*, granule vesicle; *8*, penis bulb; *9*, penis; *10*, common oviduct with attendant gland cells; *11*, common genital atrium; *12*, genital pore; *13*, bundle of ducts of frontal glands; *14*, pharyngeal cavity; *15*, bundle of gland ducts in pharynx; *16*, pharynx; *17*, esophagus; *18*, intestinal sac; *19*, granular substance inclosed in parenchymal mesh; *20*, walls of mesh; *21*, muscular septum; *22*, large type of gland cell; *23*, circular muscles; *24*, small type of gland cell.

fuchsin; the latter take on a blue color in Mallory's triple stain and hence are presumably of a mucous nature. The gland cells are typically pyriform cells filled with fine or coarse granules or rodlike inclusions; they are situated in the parenchyma and have long necks which act as ducts and discharge through an epithelium onto a free surface. Apparently in Turbellaria epithelial cells themselves never become gland cells. The caudal glands around the genital pore furnish an example of eosinophilous gland in *Hydrolimax*. Of the cyanophilous type there occur the scattered sub-epidermal cyanophilous glands which discharge through the epidermis (Fig. 3) and the frontal glands (Fig. 4). The latter form a cluster immediately behind the brain whose very long stalks run forward beneath the brain as a bundle perforating the epidermis just above the mouth opening (Fig. 7). At this place the epidermis is permeated with the exits of these glands stuffed with secretion granules. The frontal glands are of wide occurrence throughout the Turbellaria but their function is unknown. Their exits are commonly associated with a sensory epithelium as is also the case in *Hydrolimax* and hence their secretion must be of some importance, probably with regard to the capture or the swallowing of prey.

Other numerous glands of the parenchyma are associated with the reproductive system and will be described in that connection.

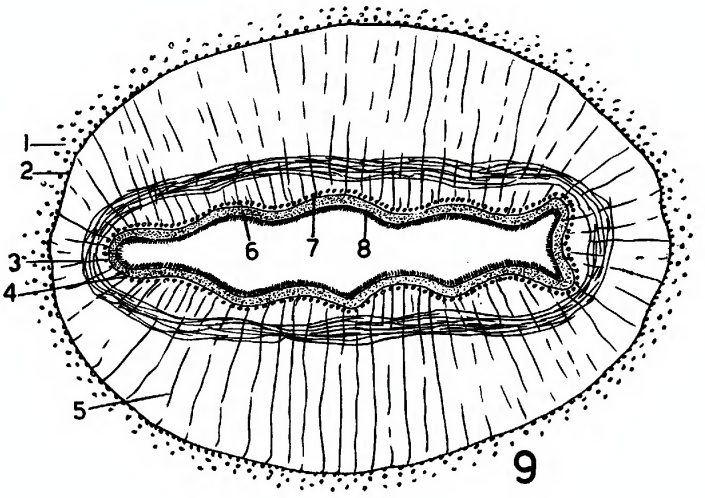
4. Digestive Tract.—A sagittal view of the digestive tract is given in figure 7. The ventral mouth leads into the small pharyngeal cavity into which projects the anterior end of the pharynx. The remainder of the conspicuous musculo-glandular pharynx is imbedded in the parenchyma and leads by a narrowed channel into the elongated blind sac of the intestine. This type of digestive tract is of course characteristic of the turbellarian orders Rhabdocoela and Alloeocoela in part.

At the entrance to the pharyngeal cavity the epidermis quickly diminishes in height, and cavity and pharynx are lined by a thin homogeneous layer in which no cell walls or nuclei can be discerned. This lining is not an "eingesenkt" epithelium, such as has been found in many Turbellaria, with nuclei sunk into the parenchyma. No nuclei can be seen in the adjacent parenchyma. The lining of the pharyngeal cavity appears to lack cilia but that of the pharynx lumen is clothed with short cilia.

The pharynx is of the bulbose type common to the Rhabdocoela and some Alloeocoela. That of the Plagiostomidae falls into the category called pharynx bulbosus variabilis by von Graff, found only in Alloeocoela. The chief distinguishing feature of the pharynx variabilis is, ac-

cording to von Graff, the inversion of the muscle layers of the periphery as compared to those next the lumen. It now appears, however, that this inversion is not present in all alloeocoels with a bulbose pharynx and in fact species of the same genus may vary in this respect. For this reason Steinböck (1923) proposed the subdivision of the pharynx variabilis into two types, intextus without the muscle layer inversion, and textus with such inversion. The pharynx of *Hydrolimax* is of the variabilis intextus type; but it is a question whether there are any real grounds for distinguishing the bulbose pharynx of alloeocoels from the doliiform pharynx of many rhabdocoels.

The pharynx of *Hydrolimax* is a compact dorso-ventrally flattened body oriented nearly parallel to the body surfaces (Fig. 7) and sharply separated from the general parenchyma by a muscular septum. The interior is filled with muscle fibers and gland cells imbedded in a scanty amount of parenchyma (Fig. 8). The lumen, as already noted, is lined by a ciliated layer devoid of cell walls or nuclei. Next this occurs a very thin stratum of longitudinal muscle fibers followed at a little distance by a thick zone of circular fibers, best seen in figure 9. No definite sphincter of circular fibers near the anterior end of the pharynx, such as has been described for other plagiostomids, was found in *Hydrolimax*. Internal to the circular layer, the pharynx is filled with gland cells, of which two sorts have been noticed, a small type near the circular muscles and a larger and more numerous type filling the peripheral half of the pharynx. The smaller kind discharge directly into the lumen along the whole length of the pharynx and their ducts filled with secretion granules can be seen passing between the muscle fibers. Some of the larger gland cells discharge in a similar way but the ducts of the majority join into a conspicuous bundle which runs forward and then curves medially to discharge *en masse* near the anterior tip of the pharynx (Figs. 7 and 8). This bundle of gland ducts is a notable feature of the *Hydrolimax* pharynx and in cross section is seen to form a circular zone in the anterior free part of the pharynx. The lining membrane of the pharynx lumen appears to be absent where the bundle of ducts discharges. The outer surface of the pharynx consists of a muscular septum in which the inner fibers are circular, the outer longitudinal. Surrounding the pharynx there is a zone of longitudinal fibers in the parenchyma, and these evidently are related to pharynx activities. A large number of radial muscle fibers extend from the pharynx lumen to its periphery (Fig. 9). There are no external gland cells attached to the pharynx. The pharyngeal glands are of the cyanophilous type.



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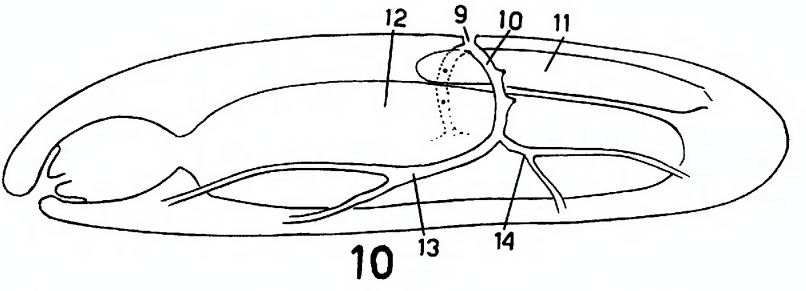

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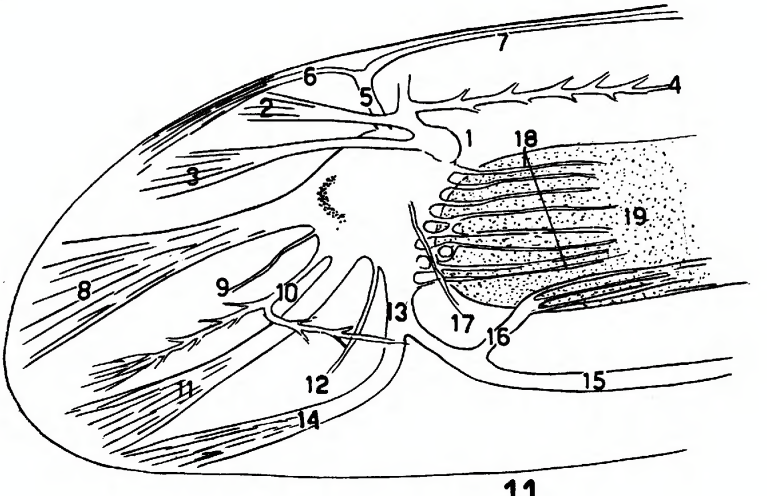

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At its posterior end the pharynx narrows to a short tube usually called esophagus (Figs. 7, 8) and at this region the pharynx lining increases in height and becomes cellular and nucleated (Fig. 8). The muscle layers next the pharynx lumen continue in diminished thickness along the esophagus.

The esophagus leads into the intestine, a simple elongated sac extending posteriorly to the copulatory apparatus. It is lined by a tall wavy epithelium (Fig. 7) which in the majority of the available preparations is syncytial without definite cell walls. A syncytial condition of the intestinal epithelium is reported as characteristic of plagiostomids by several European workers. However, in one set of sections, this epithelium is plainly cellular, composed of tall bulbous cells like those of the intestine of planarians. It therefore seems that either the intestinal epithelium of *Hydrolimax* may alter from a syncytial to a cellular state or else the cell walls commonly break down on fixation. The intestinal epithelium is highly vacuolated with basal nuclei and distal inclusions, presumably digesting food. No gland cells could be found in the epithelium. There appeared to be a few scanty muscle fibers along its outer surface.

5. Excretory System.—The main channels of the protonephridial system can be readily noticed in sections of *Hydrolimax*. The course of these vessels bears only a general resemblance to that found by Hofsten for *Plagiostomum lemani*. The chief vessels are depicted diagrammatically in figure 10. There is a main excretory pore in the mid-dorsal line at about the level of the anterior end of the granule vesicle. From this pore

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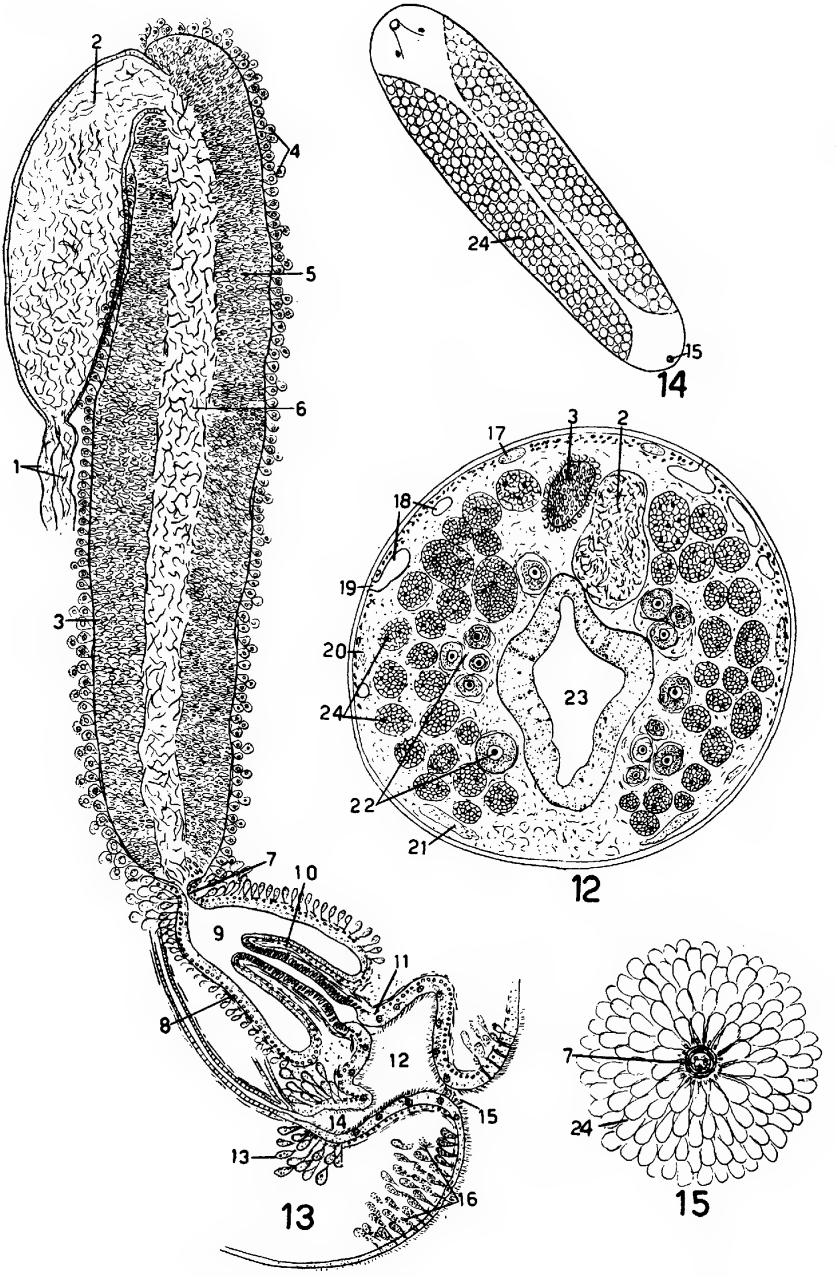
Fig. 9. Cross section through the pharynx of *Hydrolimax grisea*.

Fig. 10. Diagrammatic view of the excretory system from the side.

1, outer longitudinal muscles; *2*, outer circular layer; *3*, inner circular layer; *4*, inner longitudinal layer; *5*, radial muscles; *6*, lining syncytium; *7*, inner longitudinal layer; *8*, cilia; *9*, main mid-dorsal pore; *10*, transverse trunk with accessory pores; *11*, granule vesicle; *12*, intestine; *13*, main anterior branch; *14*, main posterior branch.

Fig. 11. Diagrammatic view of the brain and its nerves.

1, main dorso-lateral ganglion; *2*, *3*, sensory branches from same; *4*, latero-dorsal nerve; *5*, main medio-dorsal trunk; *6*, anterior sensory branch of same; *7*, dorsal body nerve; *8*, main sensory trunk to tip of head; *9*, small nerve; *10*, sensory nerve for lateral part of head; *11*, sensory nerve for antero-ventral region of head; *12*, small nerve; *13*, main ventral trunk; *14*, sensory branch of same to ventral region of head behind nerve *11; 15*, ventro-lateral body nerve; *16*, pharyngeal branch of nerve *15; 17*, small nerve; *18*, branches into pharynx; *19*, pharynx.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a large channel descends on either side in the transverse plane close to the epidermis. These transverse channels may have additional apertures to the outside (Fig. 10). In ventro-lateral regions each divides into an anterior and a posterior branch and these again subdivide into dorsal and ventral branches. The smaller channels could not be followed because of the difficulty of distinguishing them with certainty from simple parenchymal spaces but the impression was gained that the main trunks give off many small twigs. All of the larger vessels run close beneath the epidermis.

6. NERVOUS SYSTEM.—The nervous system of *Hydrolimax* is closely similar to that of *Plagiostomum lemani* described by Hofsten. The brain is a prominent bilobed mass situated above the free anterior end of the pharynx (Fig. 7). It gives off anteriorly a number of sensory nerves, some very large and conspicuous, others small and slender, and posteriorly three pairs of nerves, dorsal, lateral, and ventral as in other alloeocoels. Figure 11 depicts schematically the results of study of several sets of serial sections in which the nerves were fairly distinct. The figure makes no claim to completeness; other small nerves may have been present but I believe the main trunks are all indicated. From a dorso-lateral brain mass there springs a large nerve (Fig. 11, *1*) which gives off anteriorly two sensory branches to the dorso-lateral regions of the head (*2*, *3*) and posteriorly the lateral nerve (*4*). From the mediodorsal region of the brain arises a large trunk (*5*) which divides into an anterior sensory branch (*6*) to the mid-dorsal part of the head and a posterior trunk, the dorsal nerve. The anterior tip of the brain near the eye continues into a very massive sensory trunk (*8*) containing many ganglion cells and already mentioned as supplying a sensory area on the

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Fig. 12. Cross section through *Hydrolimax grisea* at level of transverse excretory canals.

Fig. 13. Sagittal view of terminal parts of reproductive system.

Fig. 14. Ventral view of *Hydrolimax grisea* to show distribution of yolk glands.

Fig. 15. Cross section of connecting canal with its halo of unicellular glands.

1, vasa deferentia; *2*, seminal vesicle; *3*, granule vesicle; *4*, granule glands; *5*, secretion zone of granule vesicle; *6*, central tract of sperm; *7*, connecting canal; *8*, penis bulb; *9*, cavity of penis bulb or internal seminal vesicle; *10*, penis papilla; *11*, penis sheath; *12*, common genital atrium; *13*, glands around common oviduct; *14*, cavity of common oviduct; *15*, genital pore; *16*, caudal glands; *17*, dorsal nerve; *18*, transverse excretory canal; *19*, a pore of same; *20*, lateral nerve; *21*, ventral nerve; *22*, ovaries; *23*, intestine; *24*, yolk glands; *25*, glands around connecting canal.

anterior tip just above the zone of exit of the frontal glands (Fig. 4). Ventral to this trunk there appeared to be a small nerve (*9*) which may have been part of *8*. Next comes a sensory trunk (*10*) which divides into anterior and posterior branches going to the lateral region of the head. The large sensory nerve *11* with the large branch *14* from trunk *13* completes the sensory supply of the ventral regions of the head. A small trunk *12* could not be traced very well. From the ventral part of the brain springs nerve *13* which gives off an anterior sensory branch *14* and a posterior branch *15* which becomes the ventral body nerve and gives rise near its origin to a pharyngeal branch *16*. The main nerve supply of the pharynx consists, however, of numerous nerves which pass into the pharynx directly from the posterior surface of the brain (*18*). They enter the anterior end of the pharynx and extend in the pharynx tissue near its periphery as parallel strands. These must make a circular zone in the pharynx but I was not able to detect this in cross sections. A definite nerve ring such as has been described for the pharynx of other plagiostomids appears to be absent.

The three main body nerves, *4*, *7*, and *15*, course backward throughout the body length as the lateral, dorsal, and ventral nerves, respectively, and can be seen in these positions in cross sections of the body (Fig. 12). They lie in the peripheral parenchyma near the epidermis and give off many branches.

7. Reproductive System.—The reproductive system is of paramount importance in the systematics of the Platyhelminthes and hence has received the most attention in my study since my main purpose was to establish the taxonomic position of *Hydrolimax*. The reproductive system closely resembles that of the genus *Plagiostomum*, from which it differs chiefly in the excessive length and size of the granule (or prostate) vesicle. *Hydrolimax* is of course hermaphroditic, but apparently somewhat protandrous.

The testes occur as numerous small follicles situated in the dorsolateral parenchyma opposite the anterior part of the intestine. Their connections with the vasa deferentia were not seen. The vasa deferentia can be observed only in the vicinity of the seminal vesicle where they occur as a pair of ill-defined tubules which open into the rear end of this body (Fig. 13). The seminal vesicle is a large oval structure situated dorsally at about the middle of the animal, generally to one side of the median line. The mid-dorsal region of the posterior half of *Hydrolimax* is occupied by the enormous granule vesicle, a large cylinder which extends from the copulatory apparatus to about the middle of the worm,

usually to the level of the main excretory pore. The anterior end of the seminal vesicle curves and joins the anterior end of the granule vesicle. The former is above or to one side of the anterior part of the latter. The seminal vesicle is packed with sperm which also occupy a central tract in the granule vesicle (Fig. 13) encircled by the curious secretion of the latter. This secretion has the form of closely packed ovals and presumably originates from the numerous unicellular granule glands which cover the surface of the granule vesicle (Fig. 13). The wall of both seminal and granule vesicles seems to consist of a structureless membrane.

At its posterior end the granule vesicle narrows to a short connecting canal encircled by numerous unicellular glands which joins it to a chamber called the distal sac by German workers. The latter is a conical chamber containing the penis proper or penis papilla, and in comparison with other Turbellaria would represent an internal seminal vesicle, also called true seminal vesicle, and its inclosing wall would correspond to the penis bulb. It is true this wall is less muscular than the typical penis bulb but I see no reason for inventing a new term and consequently shall call this chamber the penis bulb. It obviously must assist in the erection of the penis as is the function of the penis bulb in general among the Turbellaria. The penis papilla is a moderately elongated structure which projects into the internal seminal vesicle, that is, away from the genital pore; it obviously must turn inside out when used in copulation. This inverted position of the resting penis is common throughout the genus *Plagiostomum*. Beyond the penis bulb is another chamber, the common genital atrium, into which the penis base projects as a structure termed the penis sheath by German workers. The common genital atrium is an expanded chamber which receives in its postero-dorsal wall the common oviduct and which exits below by the common genital pore.

The histological structure of these parts is difficult to make out satisfactorily in the available preparations. The connecting canal appears to be lined by a syncytial epithelium. It is provided with obvious and well-developed muscle layers, an inner circular and an outer longitudinal and is encircled as already noted by a dense halo of large unicellular glands different from those of other parts of the male apparatus (Fig. 15). The penis bulb (distal sac of German workers) has a similar structure and is also provided with glands but these are small and of a different sort. The outer surface of the resting penis (which would be the lining layer when in use) is similar in structure to the wall of the penis bulb; but its interior (which would become the exterior at copu-

lation) differs somewhat histologically. Its lining is reduced to a mere membrane next to which is found a very thick layer of circular muscle fibers. The common genital atrium has the same structure as the general body wall, being lined by a ciliated syncytial epithelium underlain by circular and then longitudinal muscle fibers. No gland cells are attached to the atrium.

The spermatozoa are of the type characteristic of the Plagiostomidae, with a central long filamentous nucleus and winglike lateral protoplasmic expansions.

The female system is simple, consisting of ovaries, oviducts, and yolk glands without any accessory sperm-receiving chamber. The ovaries occur to either side of the gut (Fig. 12) extending forward to the pharynx. They can hardly be spoken of as a pair of definite bodies, for each consists of a number of masses which seem to have no connection with each other except presumably by way of the oviduct. The ovaries are therefore follicular like the testes. Each mass or follicle consists of a fibrous parenchyma in which there are imbedded several ova in various degrees of development. Professor Dahlgren has made a special study of ovogenesis and finds that each ovum is surrounded by a non-cellular halo presumably of nutritive nature and is attended by a cell of some size which he calls the accessory cell. I have not found a similar description for the ovaries of any other plagiostomids. The very numerous and conspicuous yolk glands occupy nearly the whole of the peripheral half of the lateral body regions from pharynx to copulatory apparatus (Figs. 12, 14). Their distribution from a ventral view is shown in Fig. 14. They are also follicular, consisting of little rounded masses each composed of several cells filled with numerous darkly staining inclusions, contained in a reticulate cytoplasm. There is an oviduct on each side running between the mass of ovarian follicles on its inner side and the mass of vitellarian follicles on its outer side. It is a ciliated tube which gives off a ciliated branch to each follicle. At the posterior end the two oviducts unite to a common oviduct, a slightly expanded chamber encircled by numerous unicellular glands; this opens into the posterodorsal angle of the common genital atrium (Fig. 13). There is no copulatory sac or seminal receptacle such as exists in many Turbellaria. Professor Dahlgren has observed the copulation, which resembles that of other Turbellaria, and has found that the penis after passing into the genital atrium through the genital pore discharges the sperm through the anterior wall of the atrium into the adjacent parenchyma. From here the sperm make their way through the parenchyma to the ovarian

follicles. In all worms examined an abundance of sperm was found in the fibrous parenchyma of the ovarian follicles. Fertilization occurs as soon as the egg is ripe and ready for discharge.

Spherical capsules resembling those of planarians are laid and attached to some object. They are red-brown in color and surprisingly large compared to the size of the worm. As in planarians these capsules containing several ova and hundreds of yolk cells are formed in the genital atrium which becomes enormously distended during their secretion. The material of the capsule comes mainly from stored droplets in the yolk cells.

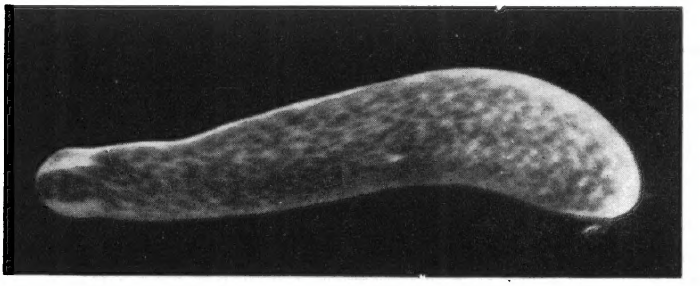

Fig. 16. *Hydrolimax grisea.* Photograph from life, by Prof. U. Dahlgren, Princeton University.

The conspicuous eosinophilous glands around the genital pore, usually known as caudal or cement glands, probably play some rôle in the laying and attachment of the capsules.

8. Taxonomic Considerations.—*Hydrolimax grisea* appears to fit into the family Plagiostomidae satisfactorily. This family is defined by Bresslau (1933) as Alloeocoela with pharynx variabilis, separate ovaries and yolk glands, follicular testes, anterior mouth, posterior common genital pore, and no accessory female structures. *Hydrolimax* differs from *Plagiostomum* in its follicular ovaries, from *Brachyposthia* in its unarmed penis, and from both in its massive granule vesicle. In external appearance *Hydrolimax* more nearly resembles *Alvaera* Bock, 1923 (= *Hallezia* Graff, 1908, preoccupied), than it does any other plagiostomid. Both have a cylindroid shape and creep upon a small part of the ventral surface. *Alvaera* also apparently has follicular ovaries and the eggs are surrounded by some sort of nutritive halo. Unfortunately the anatomy of *Alvaera* is very imperfectly known, since the only description is the old one of Jensen, 1878, luckily illustrated with some figures. From these

figures as well as Jensen's description it appears that the copulatory apparatus of *Alvaera* differs considerably from that of *Hydrolimax* having the granule complex reduced to a circle of granule glands embracing the exit of the seminal vesicle. It therefore appears that *Hydrolimax* is not congeneric with any other genus of the Plagiostomidae and even if it were, the name *Hydrolimax* has priority over all the others, so that the other names would have to be changed. No such change is necessary, however, since the characters of *Hydrolimax grisea* differ sufficiently from those of other plagiostomid species to justify the separation of this form into a distinct genus. Consequently Haldeman's name is retained as the valid name of the animal, and no other known species of Plagiostomidae are sufficiently like *H. grisea* to warrant their transfer to the genus *Hydrolimax*.

9. Generic Diagnosis of *Hydrolimax*.—Plagiostomidae with follicular ovaries and exceptionally large granule vesicle interposed between the seminal vesicle and the penis complex; otherwise similar to *Plagiostomum*. Type and only known species *H. grisea* Haldeman, 1842.

10. Distribution.—The type locality is a branch of the Susquehanna River in eastern Pennsylvania. Leidy found the animal in the Delaware and Schuylkill rivers near Philadelphia. The species at present occurs in some abundance around Princeton, New Jersey, and Dr. Charles Hadley brought me a specimen he collected near Montclair, New Jersey. Apparently *Hydrolimax* is limited to a region embracing New Jersey and eastern Pennsylvania.

11. Summary.—*Hydrolimax grisea* Haldeman, 1842, after having disappeared from notice for forty-five years has been rediscovered in New Jersey and found to be an alloeocoel of the family Plagiostomidae, the first fresh-water plagiostomid known for North America. *Hydrolimax* constitutes a valid genus of the Plagiostomidae and differs from the other genera of this family in the combination of follicular ovaries, unarmed penis, and extraordinarily large granule vesicle. In its general anatomy and histology it strongly resembles *Plagiostomum*.

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